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# The Effects of Resource Availability and Temperature on Ants

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#### **Abstract**

Body size has been strongly linked to foraging habits in ants. Running speeds, fighting ability, and thermoregulation are morphological features that influence foraging. Body mass provides a basis for the energy transfer and spatial feeding patterns throughout an ecosystem. Vapor Pressure Deficits (VPD) show larger ants typically forage at higher temperatures. However, conflicting evidence shows larger ants tend to forage at higher latitudes. Aggression among ants leads certain species to forage at less desirable times and locations. Varying resource availability allows ants to choose the most desirable resource. Additionally, foraging behavior can differ between day and night. A cafeteria-style baiting recruitment was performed in Duke Forest, North Carolina. Twelve open top chambers of 5 meters in diameter and 1.5 meters high were actively warmed to varying degrees above ambient. Additionally, 9 chamberless controls were sampled. Each chamber was baited with five resources, including: carbohydrate, oil, protein, salt, or water. Six measurements on each collected ant were taken for: head length, head width, pronotum width, Weber length, tibia length, and femur length. Significantly larger ants foraged nocturnally as opposed to diurnally. Both head length and pronotum width were significantly larger on individuals foraging on carbohydrate sources. Aphaenogaster rudis and Aphaenogaster lamellidens exhibited significantly larger head sizes among those foraging in the day. Time of day affects ant foraging habit both interspecifically and intraspecifically. Larger species of ants forage at night, but larger members of a species forage during the day. Carbohydrate is the most desirable resource among larger ants.

#### Introduction

Nature uses various methods to equip organisms for optimal opportunity to maximize calorie gain and minimize starvation possibilities. The optimal foraging theory (OFT) creates an outline that provides a better understanding of foraging behaviors by using the premise that an activity should continue to be performed until the resulting energy loss due to activity exceeds the energy gained (Macarthur and Pianka 1966). OFT has been used to specifically examine the effects of resource competition both within and between species. (Okuzaki et al. 2010). Body size and morphology is an important characteristic that has been identified as primary factor influencing the outcomes of competitive interactions and foraging behavior (Shelley et al. 2004).

Ant body sizes can vary greatly. Body morphology of ants influences types of environments that different ants will occupy. Ants of different body sizes forage at different locations, times, and on different resources (Diaz 1992). Some of this variation can be explained using physiological reasons, mainly the ectothermy of ants (Sheata and Kaschef 1971). Ants living in interstitial environments have shorter leg lengths and smaller size than those living in a planar environment (Kaspari and Weiser 1999).

Ant running speeds follow a similar pattern of increase in comparison to mammals. In general, as ant size increases, running speed also increases. This relationship has been shown to also represent the foraging speed, since the organism must move at this rate for lengthy periods of time. It represents the most energy-efficient rate, as it reflects the metabolic power available for maintaining the running motion (Hurlbert et al. 2008).

Body size also influences fighting ability of ants as depicted in the resource-holding potential (RHP) theory. Body size is one of the most important characteristics assessed during animal contests. The greater the body size and weapon size, the greater resource-holding potential a organism has. When competition over a resource exists, one group or individual will decide to withdraw from the contest due to characteristics of the other that would make the one group likely to defeat the other. Through a system of mutual assessment, ants with lower resource-holding potential will make the decision to retreat from conflict (Taylor and Elwood 2003, Batchelor and Briffa 2010). By retreating from conflict when faced against a stronger opponent, ants with lower resource-holding potential must forage in conditions that stronger opponents do not.

Thermoregulation has been shown to play a key role in determining body size distributions. Bergmann's rule, which suggests that body size is typically larger at latitudes (Bergmann 1847), is widely known to apply to endotherms. However, it is unclear as to the adherence to Bergmann's rule by insects. Some ant species have been shown to adhere to Bermann's Rule (Cushman et al. 1993), but others have not been shown to vary consistently with latitude (Geraghty et al. 2007). The heat balance hypothesis highlights patterns observed by thermoregulators which maintain body temperature and thermoconformers which have body temperatures near ambient. It shows that among thermoconformers, smaller individuals that have a higher surface to volume ratio are favored in cold climates in order to minimize heating time. This pattern influences organisms at both the interspecific and intraspecific levels (Olalla-Tarraga and Rodriguez 2007).

#### How size affects foraging

Body-mass is important in explaining the feeding structure of natural ecosystems as it provides a basis for understanding the transfer of energy within an ecosystem. Allometric degree distribution explains the relationship of body size to several other factors that affect an ecosystem. They follow the pattern that as average body mass of a species increase, the more links a species has to a resource and the fewer number of links that species has to a predator. These patterns are very important in maintaining the stability of ecosystems (Digel et al. 2011). Larger predators consume prey of greater average size and have a greater variety of prey (Gliwicz 2008).

Spatial food web body size relationships show that patterns exist for explaining feeding structure. There is a strong possibility that community level food web topology allometries and foraging behavior allometries are closely related. The body mass distribution shape is a likely reason for interconnectedness of an ecosystem's feeding structure; however, it is unclear at this point the exact relationship between the two. Therefore, it is shown that body size is a major factor for determining foraging habits (Thierry et al. 2011).

#### How temperature influences foraging

Moisture is highly linked to temperature, with higher vapor pressure deficits at warmer temperatures. It has been found that larger ants forage at high Vapor Pressure Deficits (kPa) (under drier conditions), and so larger ants typically forage at higher temperatures. It is not certain why larger ants forage at higher temperatures, but it is hypothesized that it is due to

larger energy budgets in colonies of larger ants. In these colonies, ants are forced to forage more hours of the day, therefore resulting in foraging at the peak temperatures of the day (Kaspari 1993). Looking at larger spatial scales, however, we see that larger ants tend to forage at higher latitudes, thus demonstrating evidence for use of Bergmann's Rule (Bergmann 1847, Cushman et al. 1993).

#### Interspecific competition and allocation of resources

Interspecific competition has been shown to significantly influence foraging patterns among ant species. Intraspecific aggression has been shown to increase energy support of the population and result in greater reproduction since the aggression leads them to forage longer and continue in the face of competition (Holway and Suarez 2004).

Temperature was shown to be the principle factor responsible for determining foraging patterns in ants when foraging patterns were examined across seasons (Pekas et al. 2011). Seasonal variation has also been shown to determine colony and territorial sizes, with larger populations found in the fall and smaller colony sizes in the spring. Neighboring colonies also are identified as a likely cause of variation in size of territory occupied (Tschinkel 2011).

#### **Resource affecting foraging**

It has been shown that resource distribution and availability strongly affect species abundance, richness, and composition within communities (Wilkinson and Feener 2010). Food chemical composition observed in varying nutrient availability (protein, carbohydrate, oil, salt) also affects foraging habits (Raubenheimer and Simpson 1997). Certain species of ants prefer

certain resources. Ants will forage on bait traps filled with sucrose solutions regardless of season or reproductive cycle (Choe et al. 2010). Invasive ant species such as the Argentine ant utilize carbohydrate-rich environments to displace native ant species (Kay et al. 2010). Increased carbohydrate availability also increases worker activity, thus increasing productivity (Kay and Adler 2003, Grover et al. 2007).

#### Night vs. day difference, essentially temperature difference?

Certain species of ants have been shown to forage only diurnally or nocturnally, while other species can forage throughout the day and night. Some ants may measure light levels internally as a cue to when to begin foraging (Narendra et al. 2010), while others are driven by diurnal temperature cycles. Other ants also utilize non-peak foraging hours such as early morning to forage without interference from other species (Cerda et al. 2009). Intraspecific differences in ants in daytime versus nighttime have not been well examined.

In this paper, I will examine both interspecific and intraspecific size variation among ants: 1) at various levels of warming 2) utilizing various food resources and 3) foraging in the day versus the night. I will also assess interactions between warming and these variables in regulating the size of foraging ants.

#### Methods

To examine variation in ant size along a temperature gradient and among ants recruiting to various resources, we sampled ants using a cafeteria-experiment conducted within an existing temperature manipulation experiment within Duke Forest, North Carolina. The

warming experiment consists of twelve open-top chambers 5 meters in diameter by 1.5 meters tall that are actively warmed and encompass undisturbed eastern deciduous forest. Three of the chambers are controls and maintain an air temperature within that is the same as the ambient chambers. The remaining nine chambers are set to increase the air temperature from approximately 1.5 to 5.5°C at half-degree steps. We supplemented these with an additional nine non-chamber control plots of the same diameter.

Within each chamber and chamber-less control plot, we placed four arrays of five resource solutions (sugar, protein, salt, protein, and water (control). Resource solutions were of the following concentrations: 20% sugar solution, 20% protein solution made with Jay Robb unflavored whey protein powder, 2% salt solution, 100% extra virgin olive oil, or water with nothing added. Ten ml of solution was put in a 50 ml centrifuge tube which also contained a cotton ball to soak up the solution. One tube containing each resource was arranged in a circle such that the openings were approximately 20cm apart. Of the four arrays placed in each chamber, two for three hours during the day (placed out at 11am and picked up at 2pm) and two for three hours during the night (placed out at 11pm and picked up at 2am). The two arrays present at the same time period were placed on opposite sides of the chamber from one another. For the alternate time period arrays were shifted 90° around the chamber and were again positioned opposite one another. Tubes were placed such that the opening was flat against the surface of the ground or leaf litter, allowing ants easy access to the resource. Tubes were left out for three hours before the tubes were capped and returned to the lab where all ants were identified to species.

For each species present in each resource tube collected, we haphazardly selected six individuals to measure. For tubes with fewer than six individuals of a given species, all individuals were measured. Five linear measurements were made on each ant following Kaspari (Kaspari and Weiser 1999). Head width (Joo et al. 2010) was measured as the maximum head width above the eyes. Head length (Moan et al. 2007) was taken from anterior-most portion of the clypeus to the apex of the head. Pronotum width (PW) was the maximum width of the pronotum excluding the leg tubercles. The tibia length (TL) was measured on the hind tibia. The hind femur length (FL) was measured using the length of the hind femur. The Weber length (WL) was measured using the length from the anterior-most portion of the pronotum to the posterior-most border of the metapleural lobe (Weber 1949). For each sample used in this study, a maximum of 6 individuals per species from a specific sample. An average size for the sample (± standard error) was calculated.

#### Results

Six ant species were collected commonly during baiting in this study. These species included *Aphaenogaster lamellidens*, *Aphaenogaster rudis*, *Camponotus castaneus*, *Camponotus pennsylvanicus*, *Crematogaster lineolata*, and *Formica pallidefulva*. Of these, *C. castaneus* was only observed foraging during the night and *F. pallidefulva* was only observed foraging during the day. All other species were found foraging both during the day and the night.

Considering ant size across species, we found significant differences in the size of ants foraging during the day versus the night as well as among bait types. However, temperature

treatment was not related to body size. This was true when considering both head length (time of day: F = 4.22, p = 0.04; resource: F = 3.05 p = 0.02; temperature treatment: F = 0.21, p = 0.65) and pronotum width (time of day: F = 5.86, p = 0.02; resource: F = 5.56 p < 0.01; temperature treatment: F = 0.25, p = 0.62). Leg length followed the same patterns (time of day: F = 7.48, p = 0.01; resource: F = 3.35 p = 0.01; temperature treatment: F = 1.30, p = 0.26). In general, larger ants were found on baits during the night when compared to those foraging during the day. Considering resource-type, we found larger head and pronotum widths on ants foraging on sugar than on oil. Ants foraging on salt had both larger pronotum widths and legs did ants

found foraging on oil. This suggests that smaller ant species may forage more heavily on oil.

			Head		Head		Weber
		Head	Width	Head	Length	Weber	Length
Resource	Time	Width	SE	Length	SE	Length	SE
Amino acid	Day	0.815	0.050	1.053	0.099	1.270	0.124
	Night	1.145	0.109	1.575	0.212	2.010	0.264
Carbohydrate	Day	1.233	0.128	1.461	0.148	1.899	0.192
	Night	1.428	0.118	1.670	0.165	2.309	0.259
Water	Day	0.943	0.095	1.400	0.120	1.771	0.158
	Night	1.151	0.177	1.469	0.227	2.058	0.306
Salt	Day	1.020	0.073	1.200	0.122	1.730	0.322
	Night	1.451	0.198	1.768	0.257	2.207	0.453
Oil	Day	0.985	0.041	1.198	0.082	1.517	0.129
	Night	0.970	0.033	1.058	0.063	1.476	0.134

					Leg
		Pronotum	Pronotum	Leg	Length
Resource	Time	Width	Width SE	Length	SE
Amino acid	Day	0.476	0.035	1.858	0.203
	Night	0.750	0.117	3.325	0.519
Carbohydrate	Day	0.805	0.093	3.145	0.321
	Night	0.932	0.101	3.918	0.471
Water	Day	0.671	0.064	2.957	0.389
	Night	0.770	0.144	3.604	0.647
Salt	Day	0.670	0.099	2.720	0.700
	Night	1.039	0.177	4.925	1.275
Oil	Day	0.535	0.024	2.431	0.220
	Night	0.533	0.050	2.386	0.239

Table 1: Average size ant among all species foraging on each resource. The nighttime average sizes were significantly larger than the daytime averages for all resources except oil.

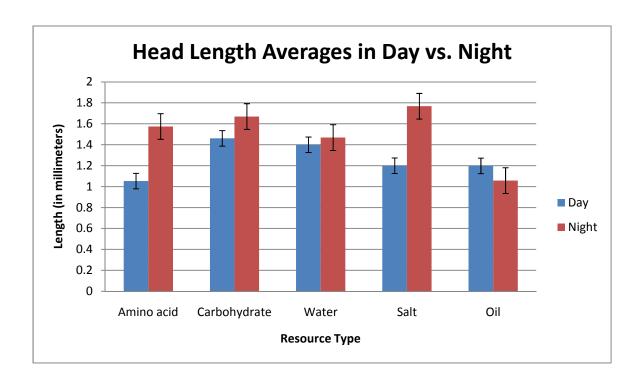


Figure 1:

Head length averages in the day (blue) and night (red) on amino acid, carbohydrate, water, salt, and oil baits. Larger ants were found foraging at night for all resources except oil.

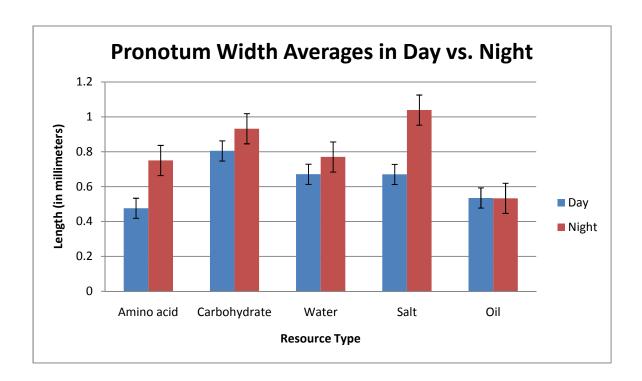


Figure 2:

Pronotum width averages in the day (blue) and night (red) on amino acid, carbohydrate, water, salt, and oil baits. Larger ants were found foraging at night for amino acid, carbohydrate, water, and salt. There was no difference in ant size foraging on oil in day or night.

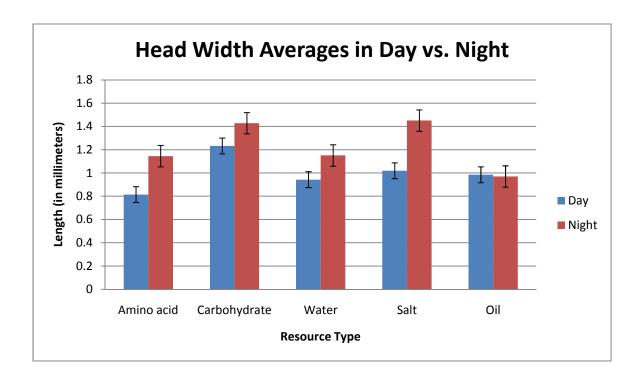
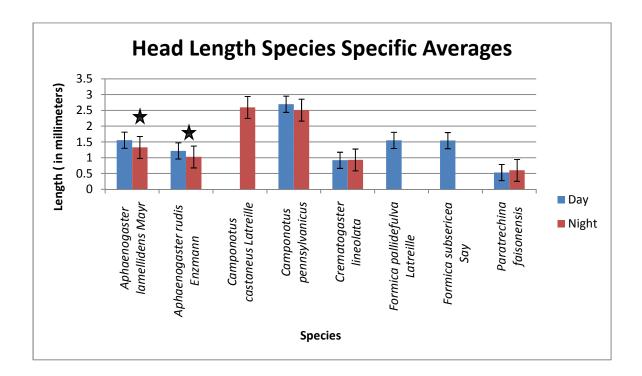


Figure 3:

Head width averages in the day (blue) and night (red) on amino acid, carbohydrate, water, salt, and oil baits. Larger ants were found foraging at night for amino acid, carbohydrate, water, and salt. Oil was shown to have larger ants foraging in the day.

Considering intraspecies size variation, we found no relationship between temperature treatment nor bait-type and size in any of the species examined. We did, however, observe significant differences between the size of ants foraging during the day versus the night within two species. Both *Aphaenogaster rudis* and *Aphaenogaster lamellidens* exhibited larger head lengths during the day than the night (*A. rudis*: F = 33.30, p < 0.0001; *A, lamellidens*: F = 41.69, p < 0.0001). Considering pronotum width, only *A. lamellidens* differed in size between day and night, which larger individuals foraging during the day (F = 9.20, p < 0.001).

Intraspecific leg length did not vary with time of day, nor temperature treatment. It did, however, very with bait type in one species. We found that individuals of *Aphaenogaster rudis* on sugar had longer legs than those we found on protein baits (F = 3.80, p = 0.01).



Head length averages in the day (blue) and night (red) for each of the species compared. Larger ants were found foraging during day for all resources across species. *Aphaenogaster lamellidens*Mayr and *Aphaenogaster rudis* Enzmann were significantly larger in the day vs. night. No significant difference was found for other represented species.

Figure 4:

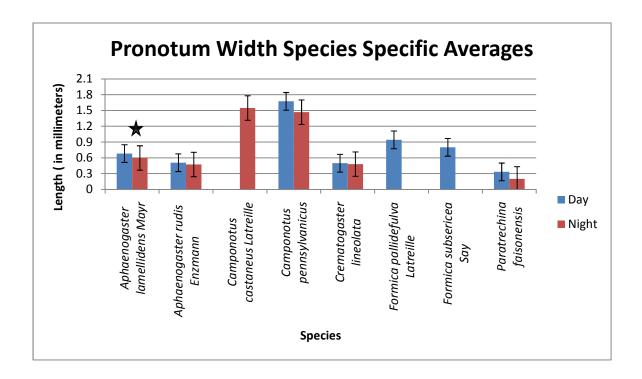


Figure 5: Head length averages in the day (blue) and night (red) for each of the species compared. Larger ants were found foraging at night for all resources. *Aphaenogaster lamellidens*, and *Aphaenogaster rudis* Enzmann were significantly larger in the day vs. night. No significant difference was found for other represented species.

#### Discussion

In this study, the differences in sizes of ants foraging on different resources at different times of the day and in different temperature environments were examined. Time of day was shown to significantly affect ant foraging habits both within and between species. Specifically, different size ants forage at different times of the day. Larger individuals to forage at night compared to daytime foragers.

Previously it has been shown that predation by arthropods occurs more often nocturnally rather than diurnally (Brust et al. 1986). Individuals of larger body size have greater resource-holding potential, which is linked to greater aggressiveness and predation (Taylor and Elwood 2003, Batchelor and Briffa 2010).

Gradual changes of temperature were not shown to effect foraging allocation of ants of different body sizes neither interspecifically or intraspecifically. None of the species observed exhibited a body size difference among temperature treatments. This suggests that ants which forage during the daytime or nighttime hours are not affected by slight changes in temperatures that occur throughout the respective period in which they forage. Even in conjunction with bait availability, temperature does not affect body size intraspecifically. This finding does not follow the same patterns observed in VPD experiments (Kaspari 1993) or in latitudinal experiments (Cushman et al. 1993). This experiment did not control for individuals from outside of the warming chamber crossing the chamber barrier and foraging on the bait and the lack of body size difference is possibly attributable to an influx of new individuals.

Larger species ants forage at night as compared with daytime hours. In the species represented here, *Camponotus pennsylvanicus* forages more heavily during the night. The peak hours of intensity for foraging are at dusk and at dawn (Nuss et al. 2005). However, larger members of *Aphaenogaster rudis* and *Aphaenogaster lamellidens* forage during the day. This pattern coincides with the findings of the VPD experiments (Kaspari 1993) and latitudinal patterns (Cushman et al. 1993) where the higher the temperature, the larger the organisms that will be found.

Kaspari found that head length and pronotum width was the best predictor of mass, and that leg length is predicted to be smaller relative to head size in small ants (Kaspari and Weiser 1999). And what did we find looking at these measurements specifically?...

Larger species forage on carbohydrate as opposed to other resources when available. As a general pattern, smaller species forage on oil. Ants with longer legs or bigger pronotum widths forage on salt if available. In *Aphaneogasater rudis* specifically, the individuals with longer legs forage on sugar and shorter legs forage on oil.

There is a link between carbohydrate foraging and behavioral dominance in invasive Argentine ants. This relationship suggests that the more dominant individual will forage on carbohydrate sources, therefore providing a hypothesis as to why larger ants are found foraging on carbohydrates (Grover et al. 2007, Kay et al. 2010).

In conclusion, we find that ant size does not vary with temperature. However, ant size does vary between nocturnal and diurnal cycles interspecifically with larger species foraging at night. Larger ants forage on carbohydrate resources. Within certain species, larger individuals foraged diurnally.

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